Summer algal blooms in shallow estuaries: Definition, mechanisms, and link to eutrophication

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Abstract

We propose a definition for identification of blooms and use this definition to investigate the underlying mechanisms of summer blooms and their link to nutrient enrichment. Blooms were defined as chlorophyll *a* observations deviating significantly from a normal seasonal cycle; the frequency and magnitude of these deviating observations characterized bloom frequency and intensity. The definition was applied to a large monitoring data set from five estuaries in Denmark with at least biweekly sampling. Four mechanisms with links to nutrient enrichment were identified as sources of summer blooms: (1) advection from biomass-rich inner estuary, (2) resuspension of nutrients and algae from sediments, (3) nutrient releases from sediments during hypoxic conditions, and (4) decoupling of benthic grazers. Summer blooms were mostly dominated by diatoms, and in 33% of the bloom samples the dominating species was also dominant prior to the bloom. Only four species (*Cerataulina pelagica, Chaetoceros socialis/radians, Prorocentrum micans*, and *Prorocentrum minimum*) typically (>50% of blooms) increased their biomass proportion during bloom initiations. Bloom frequency and intensity decreased from 1989 to 2004, corresponding to decreases in nutrient inputs and concentrations, but only bloom frequency could be directly linked to the actual total nitrogen concentrations, whereas bloom intensities depended on site-specific features, particularly a threshold response for stations exposed to hypoxia. Bloom frequency has increased over longer timescales in response to nutrient enrichment.

Phytoplankton blooms, particularly harmful algal blooms (HABs), are believed to have expanded globally in coastal waters, although there are few long-term data sets available to critically evaluate this hypothesis (Smayda 1990; Hallegraeff 1993; Cloern 2001). Phytoplankton blooms are natural phenomena that were also occurring during pristine conditions (Bianchi et al. 2000), but it has become a widespread belief that the increasing frequency of blooms is related to anthropogenic nutrient enrichment of coastal waters, although this has not been proven rigorously (Paerl 1988, 1997; Cloern 2001). For example, Dale et al. (1999) observed increasing and decreasing trends

in the abundance of dinoflagellate cysts corresponding to the signals of nutrient loading for the inner Oslofjord, and Carstensen et al. (2004) documented that interannual variations in the summer bloom frequency for the Kattegat were related to the nitrogen inputs. Particularly, the importance of atmospheric deposition (AD) as a source of 'new' nitrogen has been suggested as a primer for algal blooms (Paerl and Whitall 1999), although the relative importance of AD-N decreases with increasing mixing depth (Carstensen et al. 2005). Nutrient enrichment enhancing new production (Nixon 1995) may show as increased frequency and magnitude of phytoplankton blooms, but ecosystem attributes can act as a filter to modulate this response (Cloern 2001). This could explain why supporting evidence of the causative link to nutrient enrichment is still lacking.

A bloom is generally perceived as a significant increase in biomass, meaning there is an unbalance between phytoplankton growth and loss processes. Blooms are uncoupled from grazing and normally terminated by sedimentation (Kiørboe et al. 1996). In many cases, blooms are beneficial to food-web processes (typically "mini-blooms"), whereas excess growth and sedimentation of relatively ungrazed species, such as *Ceratium*, may contri-

bute to hypoxic conditions (e.g., Granéli et al. 1989). The trophic consequences of HABs are, however, generally seen as unfavorable to the ecosystem. Seasonal blooms, such as the spring bloom, on the contrary are regular phenomena that are connected to recurrent supply of new nutrients to the pelagic systems, and are most often terminated by sedimentation in high-latitude coastal waters (Wassmann 1990). However, the spring bloom initiation, intensity, and duration are very stochastic and driven by physical factors (Kahru and Nõmmann 1990), which makes it difficult to establish relations between spring bloom intensity and trophic status. Phytoplankton bloom dynamics rely on the synergistic interactions of favorable physical, chemical, and biotic conditions, the rates of 'new' nutrient supply being particularly important (Paerl 1988). Indeed, from a management point of view, regulating the nutrient input is the only realistic general control of bloom frequency and intensity.

In freshwater ecosystems studies have empirically connected bloom frequency to nutrient status (Walker and Havens 1995; Dokulil and Teubner 2000). There is also evidence that the *number* of bloom observations has increased in coastal environments, due to increased nutrient input or changes in the nutrient ratios favoring functional groups with most harmful and noxious species, such as cyanobacteria or flagellates (Paerl 1988; Smayda 1990; Hodgkiss and Ho 1997). However, the causal evidence that the actual *frequency* of blooms has increased due to nutrient inputs is largely lacking for coastal waters. Despite the lack of clear evidence of quantified relation, it is required to assess the ecological quality of coastal waters by means of indicators describing bloom frequency and intensity. For such indicators to become operational the causative connection to the anthropogenic nutrient enrichment must be established to allow development of type-specific assessment criteria and reference conditions (e.g., Heiskanen et al. 2004).

Before the frequency and intensity of blooms can be quantitatively described, the phytoplankton characteristics underlying a bloom must be defined. Richardson (1997) described a bloom as "the rapid growth of one or more species which leads to an increase in the biomass of the species". This and other qualitative descriptors, not having a formal definition such as "exceptional," "unusual," and "nuisance," lead to widespread confusion about what constitutes a bloom (Smayda 1997*a*). Tett (1987) used a quantitative definition of exceptional blooms as those exceeding a threshold of chlorophyll of 100 mg m^{-3}. Such a definition would not lend to many bloom observations in mesotrophic or oligotrophic waters, and it clearly contradicts the conclusion from the 1984 ICES Exceptional Plankton Bloom Meeting stating that a bloom is a deviation from the "normal cycle of phytoplankton biomass" (Parker 1987). Bloom definitions by means of exceeding biomass levels need to consider regional and seasonal scales of variation, but as Smayda (1997*a*) argues, a bloom is not simply a biomass issue, it also has a species-specific dimension. Trophic consequences of blooms vary with the species composition, particularly in the case of toxic species. According to Smayda (1997*a*) phytoplankton

blooms should therefore not be characterized by means of biomass only, but the trophodynamic effects should also be considered. Although we agree with this, in the present study for the characterization of blooms we will focus on the biomass issue only.

Here we present a general definition of phytoplankton blooms on the basis of deviations from the normal variation in biomass. It is an extension to the definition described for summer algal blooms in the Kattegat (Carstensen et al. 2004) that can be used in more dynamic estuarine and coastal waters. We have used and tested the definition on data from five estuaries in Denmark. The objective was to identify common underlying mechanisms initiating blooms and to explore potential connections to the nutrient supply. Finally, the species composition of blooms was investigated and specific opportunistic bloom species were identified.

Study sites

Danish estuarine systems are for the most part shallow (<3 m deep), have short residence times, and tend to be heavily loaded with nutrients primarily from agricultural sources (Conley et al. 2000). Tides are not a significant factor with the tidal range in Danish estuaries less than ca. 20 cm, although water level changes can be large (>1 m) under the influence of wind. Although there are no large continental-scale rivers in Denmark, freshwater inputs from streams contribute to the water balance of most Danish estuaries. In this study we selected data from nine stations under the Danish Nationwide Aquatic Monitoring and Assessment Program (DNAMAP) to investigate summer blooms (Fig. 1). Five estuaries were studied (Table 1), with the largest estuarine complex in Denmark, Limfjorden, having five stations to represent different basins.

Limfjorden is an estuarine complex that connects both to the North Sea to the west and to the Kattegat to the east, extending about 170 km. It consists of several broads connected by narrow channels. The catchment drains about 1/6 of the total Danish area with scattered stream discharges throughout the entire estuary. Stratification occurs through intrusions of saline North Sea water through the western inlet propagating to the other broads, but it is easily broken down by wind mixing in the shallow parts. The western part has broad shoals on both sides of the central channel and is more exposed to wind than other basins. The central parts of Limfjorden, particularly the basin represented by station 3727, are exposed to hypoxia almost every summer.

Horsens Fjord and Vejle Fjord have adjacent catchments of similar magnitude (Fig. 1) and the physical characteristics are also similar, except that Vejle Fjord is slightly deeper (Table 1). Most of the freshwater (>75%) is discharged from streams to the inner shallow parts. Both estuaries broaden and deepen from head to mouth where water exchange with the North Belt is not restricted. Bottom water from the North Belt (pycnocline ~15 m depth), rich in nutrients and low in oxygen during summer, occasionally intrudes into the estuaries.
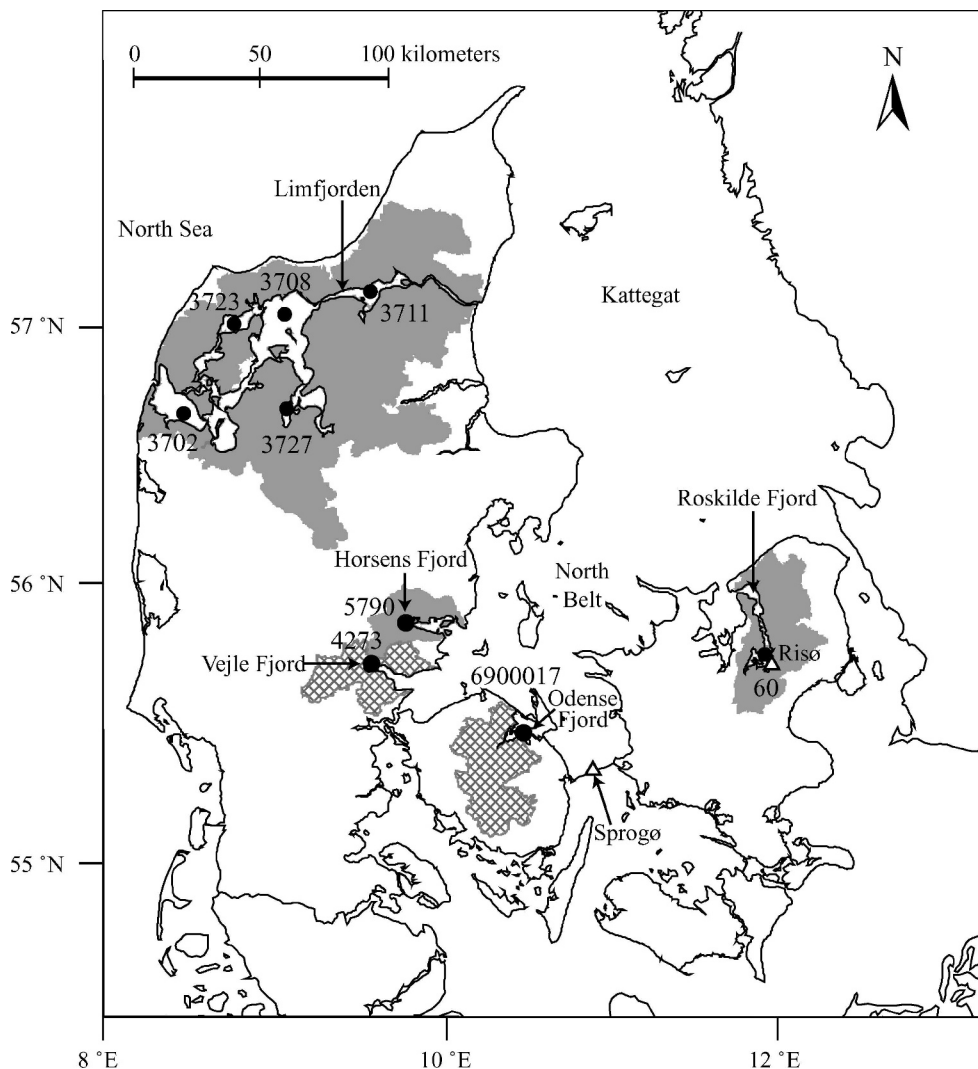
Fig. 1.   The five Danish estuaries studied with identification of monitoring stations. Shaded areas show the catchments for each of the estuaries. Meteorological stations at Sprogø and Risø with wind speed measurements are labeled by triangles.

Odense Fjord is the shallowest of the study sites and consists of two basins, where the inner part and outer parts have mean depths of 0.8 m and 2.7 m, respectively. The monitoring station is located in the outer part of the estuary. Odense Fjord has a central channel and wide broad shoals covered by eelgrass (*Zostera marina*) and macrophytes. The estuary has the lowest residence time of the study sites and freshwater input is dominated by the

River Odense. Water exchange with the North Belt takes place through a narrow inlet.

Roskilde Fjord is a long-stretched estuary (~40 km) with many small streams discharging along the entire course. The largest water volume is contained in the inner part, where the monitoring station is located, and the water course consists of deep channels interrupted by shallower banks, acting as sills on the water exchange. There are large

Table 1.   Physical and nutrient input characteristics of the five studied estuaries. Nutrient discharges were average values for 1989–1995 (Kaas et al. 1996). Hydraulic residence times (winter period) were estimated in Rasmussen and Josefson (2002).

Estuary	Area (km^2)	Volume (km^3)	Mean depth (m)	Max depth (m)	Catchment area (km^2)	TN input (10^6 kg yr^{-1})	TP input (10^6 kg yr^{-1})	Residence time (d)
Limfjorden	1517	7.486	4.9	28.0	7590	18.330	0.436	—
Horsens Fjord	78.2	0.234	3	20.6	449	1.678	0.038	15
Vejle Fjord	107.8	1.084	10.1	20.7	732	2.260	0.101	18
Odense Fjord	61.8	0.106	1.7	10.9	1057	2.849	0.072	7
Roskilde Fjord	124.8	0.371	3	30.7	1176	1.600	0.135	90

horizontal salinity gradients but the water column is generally well-mixed with temperature stratification potentially occurring during calm periods. Compared to the other study sites land use in the Roskilde Fjord catchment is more urbanization and less agriculture.

Materials and methods

Sample collection—Data on salinity, temperature, oxygen, nutrients, chlorophyll *a* (Chl *a*), and phytoplankton biomass by species were selected from nine monitoring stations under DNAMAP. These stations, representing shallow estuaries, have been sampled frequently (at least biweekly) for 6–16 yr for hydrochemistry, and less frequently for phytoplankton by the Danish counties (Table 2). Water column salinity, temperature, and oxygen concentration were measured by CTD and stored with a 0.2-m resolution, and surface and bottom water (if stratified) were sampled for hydrochemistry. Nutrients were measured by standard wet chemical techniques, and Chl *a* was measured by trichromatic spectrophotometry.

Phytoplankton was collected as an integrated sample of the euphotic zone (down to 1% surface light) either combined from various discrete water samples or collected using an integrating hose. Direct counts and measurements of dimensions of phytoplankton were made in an inverted microscope on Lugol-fixed samples according to Utermöhl (1958). Phytoplankton carbon biomass was calculated from cell counts and dimension measurements assuming simple geometric shapes and using conversion factors of 0.13 and 0.11 pg μm^{-3} for thecate dinoflagellates and other phytoplankton groups, respectively. Carbon contents of diatoms were corrected for lower C content of cell vacuoles (pg [μm^3 vacuole]$^{-1}$ = 0.1×pg [μm^3 plasma volume]$^{-1}$) according to Edler (1979).

Potential two-layer stratification and the resultant depth of the pycnocline were examined by fitting a sigmoid function (the normal cumulative distribution function, PROBIT) to the density profile, calculated from salinity and temperature at discrete depths of 0.2 m resolution. If a well-defined fit was obtained ($p < 0.05$) the water column was valued as stratified, otherwise mixed. Average concentrations of Chl *a*, dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), dissolved silicate (DSi), total nitrogen (TN), and total phosphorus (TP) for the water column were calculated, in case of stratification by weighting surface and bottom water samples with the water volume they represented.

Wind speed observations were obtained from two separate and partly overlapping time series at Sprogø located in the middle of the Great Belt (data source: Sund and Bælt Holding A/S) and Risø near Roskilde Fjord (data source: Dept. of Wind Energy, Risø National Laboratory). Both time series had a temporal resolution of 10 min. For each of the two time series daily averages of wind speed were calculated. These daily values were compared for the overlapping time period of the two time series by calculating the mean difference and recalibrating the Risø data to the Sprogø time series. A combined time series was obtained by averaging over the Sprogø and the recalibrated Risø daily values.

Bloom frequency and intensity—Chl *a* observations were assumed to derive from two separate station-specific distributions, nonbloom and bloom observations. Nonbloom observations were described by means of a normal distribution with a mean having an interannual and a seasonal component

$$\mu_t = year_i + a \cdot \cos\left(\frac{2\pi \cdot t}{365}\right) + b \cdot \sin\left(\frac{2\pi \cdot t}{365}\right) \qquad (1)$$

where $year_i$ is the yearly mean value and t is the day number within the given year. The variance (σ^2) of nonbloom observations was constant. Chl *a* observations were partitioned into nonbloom and bloom observations by means of an algorithm where initially all observations were assumed to belong to the nonbloom distribution. The model (Eq. 1) was estimated using all nonbloom observations and Chl *a* observations exceeding the 99th percentile of the prediction interval ($\hat{\mu}_t + t_{99\%,edf} \times \hat{\sigma}$, edf = error degrees of freedom) were categorized as bloom observations. The model was iteratively re-estimated until all nonbloom observations were below the 99th percentile of the prediction interval. For a large number of observations

Table 2. Depth, period, number of observations (days of sampling) of Chl *a*, and phytoplankton biomass for stations used in the present study.

Station	Depth (m)	Period	$n_{Chl a}$		$n_{phytoplankton}$	
			All	Summer	All	Summer
3702	6.5	1993–2004	465	175	322	135
3708	7.3	1993–2004	364	132	321	133
3711	8.0	1998–2004	173	60	—	—
3723	11.0	1998–2003*	151	51	—	—
3727	5.0	1993–2004	486	182	326	136
4273	7.0	1993–1997, 2004	186	76	188	75
5790	3.5	1995–2004	405	143	260	101
60	4.8	1993–2004	451	170	323	137
6900017	8.4	1989–2004	967	321	178	62

* Station was discontinued in 2004.

($n > 100$) the 99th percentile of the normal distribution (= 2.33) can be used instead of the t-distribution.

The bloom frequency of a given period was calculated as the number of bloom observations divided by the total number of Chl a observations. Bloom intensity was calculated as the deviation of bloom observations from the expected mean concentration (observation $- \hat{\mu}$) as opposed to considering the absolute Chl a concentration (Edwards et al. 2003). The bloom frequency and average bloom intensity was calculated for each summer period (May–August), i.e., for each combination of station and year.

Statistical analysis—The partitioning of Chl a observations into blooms and nonblooms resulted in a binomial variable that was analyzed in relation to stratification patterns (stratified/mixed), physical and chemical measurements, as well as wind conditions before the observation. Bloom intensity observations were approximately lognormally distributed. To investigate if blooms were generally occurring simultaneously and with similar magnitude across the different stations, observations were compared if sampled during the same week. The co-occurrence of blooms was investigated by means of 2×2 contingency tables for all combinations of stations using a chi-square test to investigate if the frequency of bloom at one station was higher if a bloom was observed at another station. For log-transformed bloom intensities Pearson's correlations were calculated and tested with a t-test. The potential relation between summer bloom frequency and intensity was investigated by calculating Pearson's correlations of station-specific summer averages.

Differences in salinity, temperature, nutrients, and bottom oxygen as well as bottom oxygen concentration of the previous sample were investigated by means of analysis of variance (ANOVA) including three factors to describe bloom and stratification conditions in addition to a seasonal component. Nutrient concentrations (DIN, DIP, DSi, TN, and TP) were log-transformed before the analysis. Mean differences in the hydrophysical and hydrochemical components for blooms versus nonblooms were calculated taking the variations of the other factors into account. For the log-transformed nutrient concentrations the mean difference described a relative change, whereas absolute changes were calculated for the other variables. Differences in wind conditions before bloom/nonbloom observations were similarly calculated by means of a two-way ANOVA including a seasonal component.

Bloom frequency and bloom intensity were analyzed within the framework of generalized linear models (McCullagh and Nelder 1989) by means of the binomial (link function PROBIT) and lognormal distributions (link function identity), respectively. The significance of different factors in the models was analyzed by means of the likelihood ratio test (chi-square distributed). Summer values for all stations combined were calculated as marginal means from a model with station and year as categorical factors. Temporal trends were investigated by changing year into a quantitative factor using the same

general model. The effect of stratification patterns on bloom frequency and intensity was investigated with a two-factor model describing seasonal variations by monthly means and stratification of the present sample, or, alternatively, stratification of the previous sample.

Phytoplankton samples were combined with the bloom observations based on Chl a, and the frequency of species dominating bloom observations was calculated to identify the most common bloom species. The biomass of phytoplankton species was aggregated into three functional groups (diatoms, dinoflagellates, and other species), and the dominating species in terms of biomass contribution was determined for each sample. The biomass proportion of the dominating species was related to the total phytoplankton biomass by means of nonlinear regression using a sigmoid function (PROBIT). The change in phytoplankton composition during a bloom initiation was analyzed by identifying phytoplankton samples observed before a bloom observation (≤ 14 d prior). The group-specific and species-specific changes were investigated by calculating the frequency of increasing biomass (group only) and proportion (group and species level) and comparing this to an expected frequency of 50% (random chance) by means of a sign test. Finally, the frequency of bloom initiations where the dominating species was identical in the bloom sample and the previous sample was found.

Results

Bloom identification—Applying the bloom definition to the entire data set resulted in 616 blooms of 3,648 Chl a observations ($\sim 16.9\%$), including both spring and autumn blooms. For the summer months (May–August) these numbers were 231 blooms of 1,310 Chl a observations ($\sim 17.6\%$). The algorithm, converging after 17 iterations, clearly classified many unusually high Chl a observations as well as observations that were marginally above the threshold given by the 99th percentile (Fig. 2). The station-specific summer bloom frequency for the entire study period varied from 10.5% at station 4273 to 24.2% at station 3708, and 7 of the 35 pairwise tests showed an increased probability of a bloom observation, provided that a bloom was observed at another station (Table 3). It should be stressed that an average of two tests would crop out significantly by shear randomness. Particularly, two stations in Limfjorden, 3708 and 3727, were frequently having blooms in the same weeks, e.g., there was 62.5% probability of observing a bloom at station 3727 if a bloom was observed at station 3708, and similarly there was 71.4% probability of observing a bloom at station 3708 if a bloom was observed at station 3727. Less significant correlations were found between station 3723 and stations 3727, 5790, and 60, between station 3708 and 6900017, and between station 4273 and stations 5790 and 6900017. The blooms at station 3702 as well as station 3711 appeared completely uncoupled in time to those observed at the other stations (Table 3).

Summer bloom intensities varied from 3.2 to 82.6 μg L^{-1} Chl a (all observations). The station-specific distributions
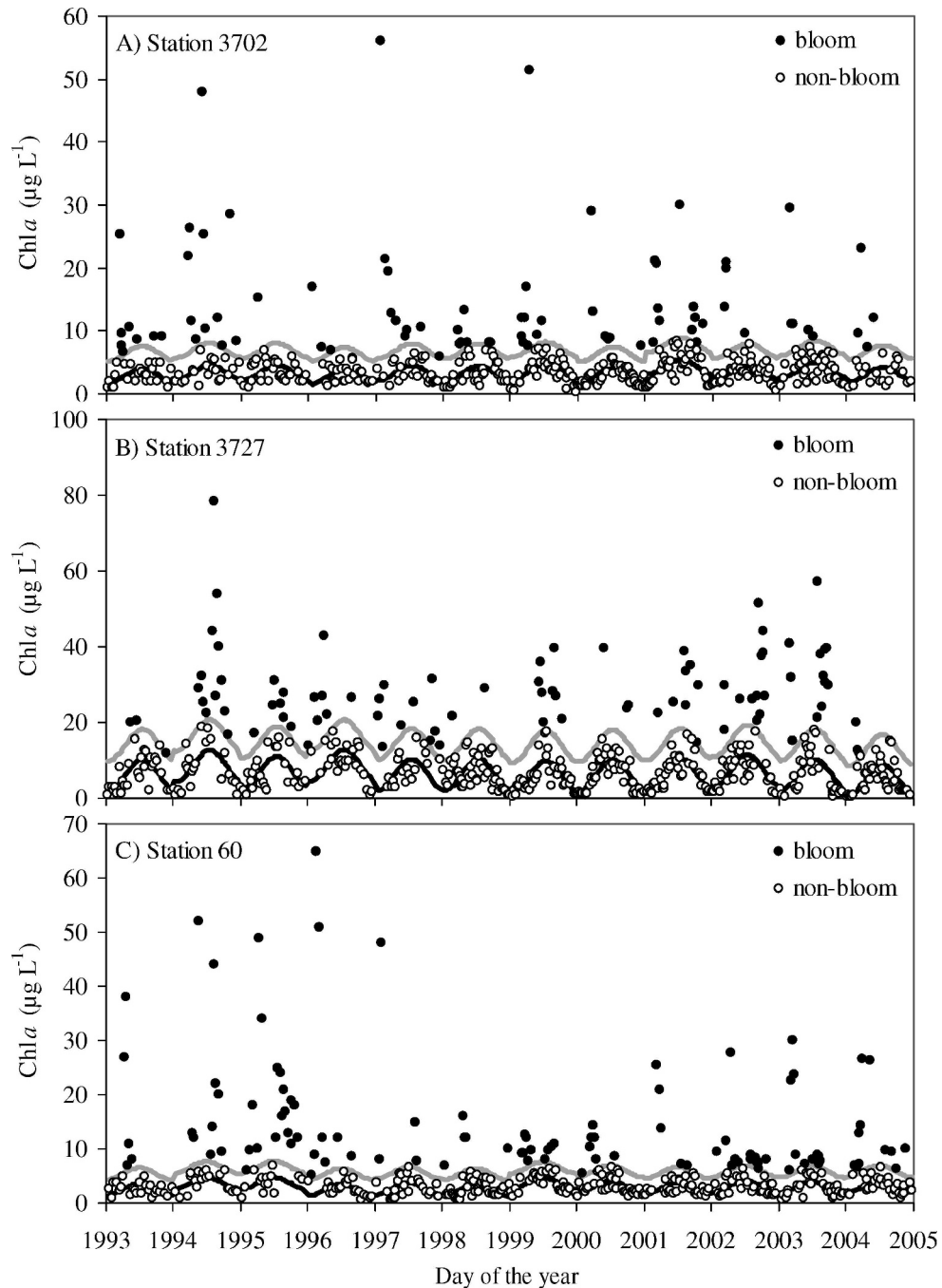
Fig. 2. Time series of Chl *a* partitioned into bloom and nonbloom observations exemplified for three stations with (A) a relatively low bloom frequency, (B) an average bloom frequency, and (C) a relatively high bloom frequency. The solid dark and gray lines show the mean and the 99th percentile of the prediction interval, respectively. In (B) three observations were outside the plotting range (207, 127, and 137 μg L^{-1} Chl *a* observed at 1st, 8th, and 15th September 1997). Note the difference in scales.

were right-skewed with comparable average intensities for seven stations ranging from 7.1 μg L^{-1} Chl *a* at station 6900017 to 10.0 μg L^{-1} Chl *a* at station 60, whereas the average values were much higher for station 3723 (22.5 μg L^{-1} Chl *a*) and station 3727 (20.5 μg L^{-1} Chl *a*). There were no significant correlations between

observations from different stations recorded in the same week, such that the bloom magnitude was not related to the bloom intensity at other stations ($p > 0.05$ for all correlations of log-transformed intensities). There was no significant correlation between summer bloom frequency and intensity, for neither stations individually nor for all

Table 3. Probability (in percentages) of observing a bloom at stations given by column names given that a bloom was observed at the station in the first column, i.e., Prob(bloom at station$_j$|bloom at station$_i$). The average summer bloom frequency is shown in the last row. Significantly different probabilities from the expected average probability are accentuated in bold (* $p<0.05$, ** $p<0.01$, and *** $p<0.001$).

Station$_j$ Station$_i$	3702	3708	3711	3723	3727	4273	5790	60	6900017
3702	—	43.7	33.3	0.0	22.7	14.3	7.7	11.8	18.2
3708	21.8	—	37.5	25.0	**62.5***	11.8	0.0	30.8	**31.3***
3711	20.0	33.3	—	11.1	20.0	—	10.0	25.0	30.0
3723	0.0	33.3	16.7	—	**50.0***	—	**33.3****	**50.0***	0.0
3727	14.3	**71.4****	28.6	**37.5***	—	21.4	10.0	35.7	24.2
4273	20.0	40.0	0.0	—	50.0	—	**66.7***	42.9	**50.0***
5790	7.7	0.0	14.3	**66.7****	14.3	**28.6***	—	26.7	29.4
60	6.0	30.8	18.2	**33.3***	29.4	23.1	14.8	—	18.0
6900017	13.8	**41.7***	37.5	0.0	26.7	**26.7***	25.0	23.3	—
Average	12.6	24.2	16.7	11.8	19.2	10.5	12.6	22.9	19.0

stations together (Fig. 3). This decoupling of bloom frequency and intensity was also apparent for the annual values for all nine stations combined (Fig. 4) having a correlation of $r = 0.02$ ($p = 0.94$). However, both summer bloom frequency ($\chi^2 = 8.51$, $p = 0.0035$, $n = 93$, df = 1) and summer bloom intensity ($\chi^2 = 8.16$, $p = 0.0043$, $n = 231$, df = 1) decreased significantly during the 16-yr study period (Fig. 4).

Covariation analysis—The frequency of stratification ranged from 0% (always mixed) at the shallow station 5790 to 40% at station 3727 in the inner branch of Limfjorden (Fig. 5). The probability of observing a summer bloom appeared related to stratification patterns for two stations only, although not significant. There was a slightly increased probability of summer blooms at station 3702 if the water column was mixed ($\chi^2 = 3.21$, $p = 0.0730$, $n = 175$, df = 1) and if the water column in the previous sample was mixed ($\chi^2 = 2.88$, $p = 0.0896$, $n = 175$, df = 1). Only

three stations (3708, 3727, and 6900017) had sufficient observations of bloom intensities under different stratification regimes to truly assess differences (at least five observations in each group), and bloom intensities were significantly higher during stratified conditions (66.6%) at station 3708 only ($\chi^2 = 5.87$, $p = 0.0154$, $n = 32$, df = 1).

TN and TP concentrations were generally higher for bloom than for nonbloom observations, with significant increases of 25% to 48% at 9 of 18 tests (Table 4). The smallest increases in total nutrients were observed at stations 3711, 4273, and 60 that on the contrary had the largest decreases in DIN and DIP of 20% to 57% (3 of 6 tests significant). Considerable decreases in DSi (from 45% to 60%) were also observed in the central and eastern part of Limfjorden (stations 3708, 3711, 3723, and 3727) and in Vejle Fjord (station 4273). Blooms were characterized by lower salinity at all stations, but the decrease was only significant for three stations (3711, 4273, and 6900017). Temperature was mostly higher during blooms than
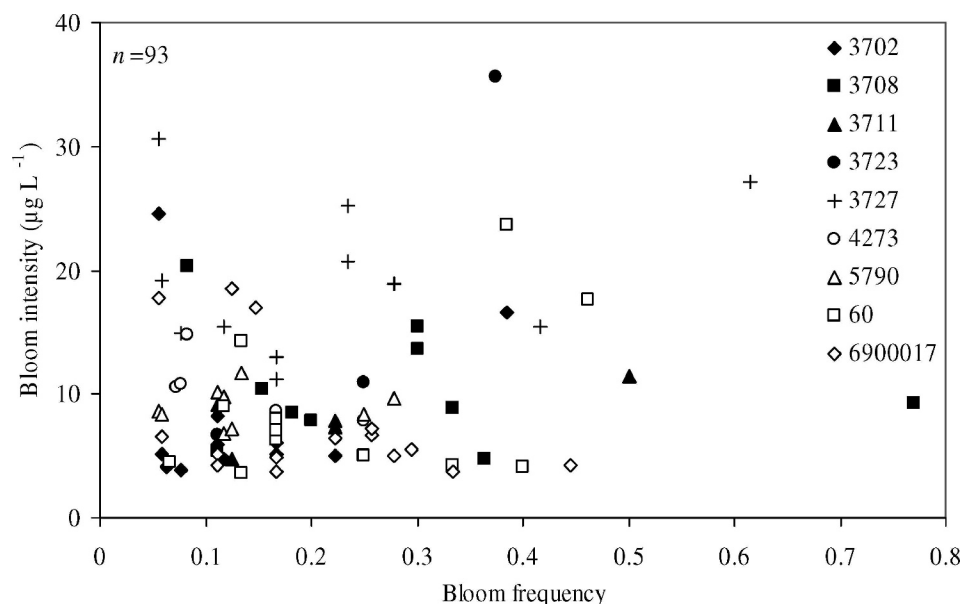

Fig. 3. Summer bloom frequency versus average bloom intensity for the nine stations combined (93 summer values).
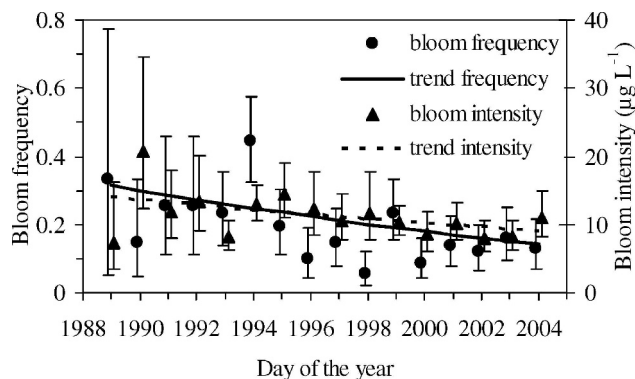
Fig. 4. Summer bloom frequency and intensity (May–August) of all stations combined. Means and 95% confidence limits for the means (error bars) as well as trends were estimated from the generalized linear models and back-transformed.

nonbloom observations, although only significant at two stations (3727 and 6900017). The oxygen concentration near the bottom did not change significantly at any station (Table 4) although the observed decrease at station 3723 was substantial (from mean values of 5.94 mg L^{-1} during nonblooms to 4.30 mg L^{-1} during blooms). Two stations had a significantly lower bottom oxygen concentration in the previous sample, mean values changing (nonbloom to bloom) from 6.05 mg L^{-1} to 4.74 mg L^{-1} at station 3727 and from 7.88 mg L^{-1} to 7.45 mg L^{-1} at station 6900017.

Wind speed was significantly higher 1–3 d before bloom observations at station 3702 (Table 4), corresponding to increased frequency of blooms during mixed conditions (Fig. 5). Blooms at station 3711 typically occurred 4–7 d after calm wind conditions, whereas blooms at station 3723 occurred 4–6 d after stronger winds. Blooms in Horsens Fjord (station 5790) were observed with a mean wind speed

of 1.2 m s^{-1} less than for nonbloom observations, whereas blooms in Roskilde Fjord (station 60) were preceded by calm winds up to 3 d prior. Differences in wind conditions between bloom and nonbloom observations were small (<1 m s^{-1}) for the other stations.

Phytoplankton bloom species—The 779 phytoplankton samples during the summer period (Table 2) were partitioned into 140 blooms and 630 nonbloom observations. There were nine phytoplankton samples without corresponding Chl *a* observations. Two stations, 3711 and 3723, did not have phytoplankton samples after 1998 and were not used in the bloom species analysis. Summer blooms were mainly dominated by diatoms (76 blooms), particularly *Skeletonema costatum*, which had the highest biomass in 32 of 140 samples (23%, Table 5). Species such as *Coscinodiscus* sp., *Prorocentrum minimum*, and the autotrophic ciliate *Myrionecta rubra* (=*Mesodinium rubrum*) were also frequently dominating species during blooms. These four taxa dominated the biomass of almost 50% of all summer blooms (69 of 140). The proportion of biomass contributed by the dominating species ranged from as low as 18% to almost 100%, and exceeded 50% in 93 of the 140 samples (66%). The proportion of the dominating species generally increased with the total biomass (Fig. 6), and the relation did not differ from bloom to nonbloom observations ($\chi^2 = 2.73$, $p = 0.2555$, $n = 770$, df = 2). However, there were large differences in the species-specific relation (Fig. 7), showing that the four most common bloom species dominated in different ranges of total phytoplankton biomass and that *S. costatum, M. rubra*, and *P. minimum* were increasing their proportion of biomass significantly with increasing biomass, whereas *Coscinodiscus* sp. dominated at relatively low biomasses without increasing its proportion with increasing biomass. Particularly, *P.*
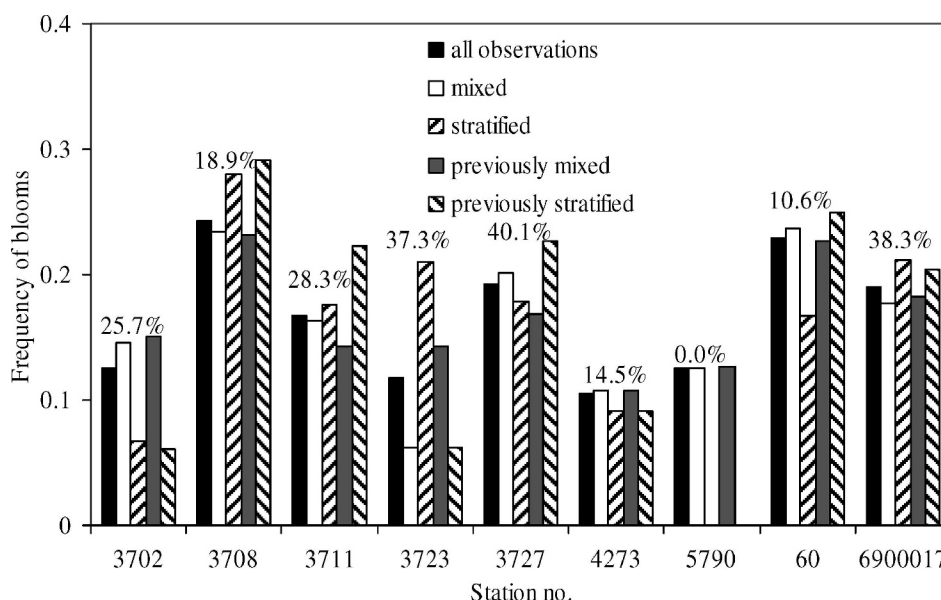

Fig. 5. The average frequency of summer blooms for all observations, under stratified and mixed conditions, and under stratified and mixed conditions of the previous sample. The station-specific frequency of stratification is given above the bars.

Table 4. Differences in nutrients (on the basis of log-transformed observations), salinity, temperature, bottom oxygen in present and previous sample, and wind speed prior to observations (up to 10 d) between bloom and nonbloom observations. Significant differences are accentuated in bold. An average of 5% of the tests will be significant by randomness (type I error) even if there is no difference.

Covariation variable	Unit	Station 3702	3708	3711	3723	3727	4273	5790	60	6900017
DIN	%	7	30	−20	25	29	−42	−2	**−49**	−20
DIP	%	3	−24	**−50**	−21	−6	−57	**65**	**−49**	21
Dsi	%	21	**−52**	−45	−46	**−60**	−48	14	5	13
TN	%	10	**25**	19	16	**34**	22	**23**	7	**32**
TP	%	**39**	21	18	**41**	**48**	14	**48**	−17	**22**
Salinity		−0.33	−0.69	**−1.61**	−0.51	−0.45	**−6.23**	−1.27	−1.01	**−0.90**
Temperature	°C	−0.57	0.63	1.11	−0.33	**0.85**	3.09	0.39	1.14	**1.11**
Bottom O$_2$ (t)	mg L^{-1}	0.18	−0.69	0.06	−1.64	−0.05	−0.52	−0.42	−0.19	−0.16
Bottom O$_2$ ($t-1$)	mg L^{-1}	0.32	−0.80	0.18	−0.50	**−1.31**	0.80	−0.10	0.38	**−0.43**
WS (0 d)	m s^{-1}	0.0	0.1	1.4	0.5	0.4	0.1	**−1.2**	**−1.6**	0.3
WS (−1 d)	m s^{-1}	**2.1**	0.2	0.3	−0.3	0.2	−0.3	−0.2	**−1.4**	−0.3
WS (−2 d)	m s^{-1}	**1.2**	0.6	0.4	−0.7	−0.4	−0.2	0.2	**−1.1**	**−0.8**
WS (−3 d)	m s^{-1}	**1.0**	0.4	0.1	0.2	0.2	−0.1	−0.1	**−0.8**	**−0.6**
WS (−4 d)	m s^{-1}	−0.2	0.3	−1.1	1.4	0.2	0.3	−0.3	−0.2	−0.4
WS (−5 d)	m s^{-1}	0.4	−0.3	**−1.8**	**2.2**	0.0	−0.2	0.4	−0.6	**−0.9**
WS (−6 d)	m s^{-1}	−0.1	**−0.9**	**−2.1**	1.9	−0.8	−0.2	0.0	−0.7	**−0.7**
WS (−7 d)	m s^{-1}	0.1	−0.9	−1.4	−0.5	−0.8	−0.7	−0.1	−0.7	−0.2
WS (−8 d)	m s^{-1}	0.1	**−0.9**	−0.3	−0.7	−0.5	−1.0	−0.5	−0.1	−0.2
WS (−9 d)	m s^{-1}	−0.4	−0.1	0.3	0.4	−0.1	0.5	0.6	−0.3	0.0
WS (−10 d)	m s^{-1}	0.1	−0.5	−0.2	−0.2	0.0	1.2	0.4	−0.7	−0.3

minimum dominated high biomasses only, with a gradient two to four times higher than for the other species (Fig. 7).

A total of 78 bloom initiations were identified where the nonbloom observation was sampled no more than 14 d before the bloom observation. At group level diatoms and dinoflagellates significantly increased their biomass during bloom initiation (56 times of 78, $p < 0.0001$ and 51 times of 76, $p = 0.0038$, respectively), whereas other species mostly increased their biomass, although not significantly (48 increases of 78, $p = 0.0535$). However, only diatoms

Table 5. Number of occurrences that each species contributed the highest biomass to summer phytoplankton blooms. Dominant bloom species recorded only once are not shown.

| Functional group and species identification	Station 3702	3708	3727	4273	5790	60	6900017
Diatoms							
Cerataulina pelagica	2	2	3		1		
Chaetoceros socialis/radians		3	3				
Coscinodiscus sp.	1	1				8	
Nitzschia sp.	2	1					
Pseudo-nitzschia delicatissima		1		2			
Rhizosolenia fragilissima	2	2	3				
Skeletonema costatum	1	3	6	5	6	6	5
Thalassiosira sp.	1	2					
Dinoflagellates							
Gymnodinium sanguineum			1	1			
Heterocapsa rotundata		1				1	
Heterocapsa triquetra						2	
Prorocentrum micans			3				
Prorocentrum minimum			3	4	1		1
Other species							
Cryptophyceae			2			2	
Dictyocha speculum	2						1
Myrionecta rubra	2	5	3			7	
Monads						8	
Pyramimonas sp.						2	
Total	16	32	28	7	10	37	9
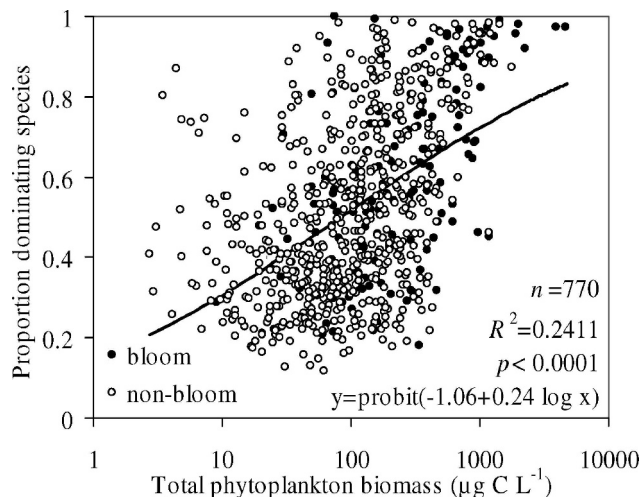
Fig. 6. Biomass proportion of the dominating species versus total biomass for all phytoplankton samples (140 blooms and 630 nonblooms). Total phytoplankton biomass is on logarithmic scale.

increased their proportion of the biomass during bloom initiation (48 increases of 77, $p = 0.0395$), dinoflagellates neither increased nor decreased their proportion (39 increases of 76, $p = 0.9088$), and other species decreased their proportion in most cases (21 increases of 78, $p < 0.0001$).

At the species level *Skeletonema costatum* had the largest average increase in biomass proportion during bloom initiation as defined here, but the probability of increasing its proportion was only slightly higher than and not significantly different from 50% (Table 6). In fact, *Cerataulina pelagica*, *Chaetoceros socialis/radians*, *Prorocentrum micans*, and *Prorocentrum minimum* were the only species that had probabilities of increasing their biomass proportion significantly larger than 50%. All other species did not have a probability exceeding 50% of increasing their biomass proportion. Both diatoms and dinoflagellates were included among the most common species that generally increased their biomass proportion during bloom initiation (Table 6). The relatively high proportion of the dominating species (mostly above 50%, Fig. 6) combined with the moderate changes in biomass proportion at bloom initiation suggests that the bloom-dominating species was relatively abundant before the bloom. In fact, in 26 of the 78 bloom initiations (33%) the dominating species during the bloom was also dominating before the bloom.

Discussion

There are many different views on what level of biomass or cell numbers actually constitutes a phytoplankton bloom (see discussion in Smayda 1997*a*). Smayda (1997*a*) disadvocated the use of a biomass criterion for defining
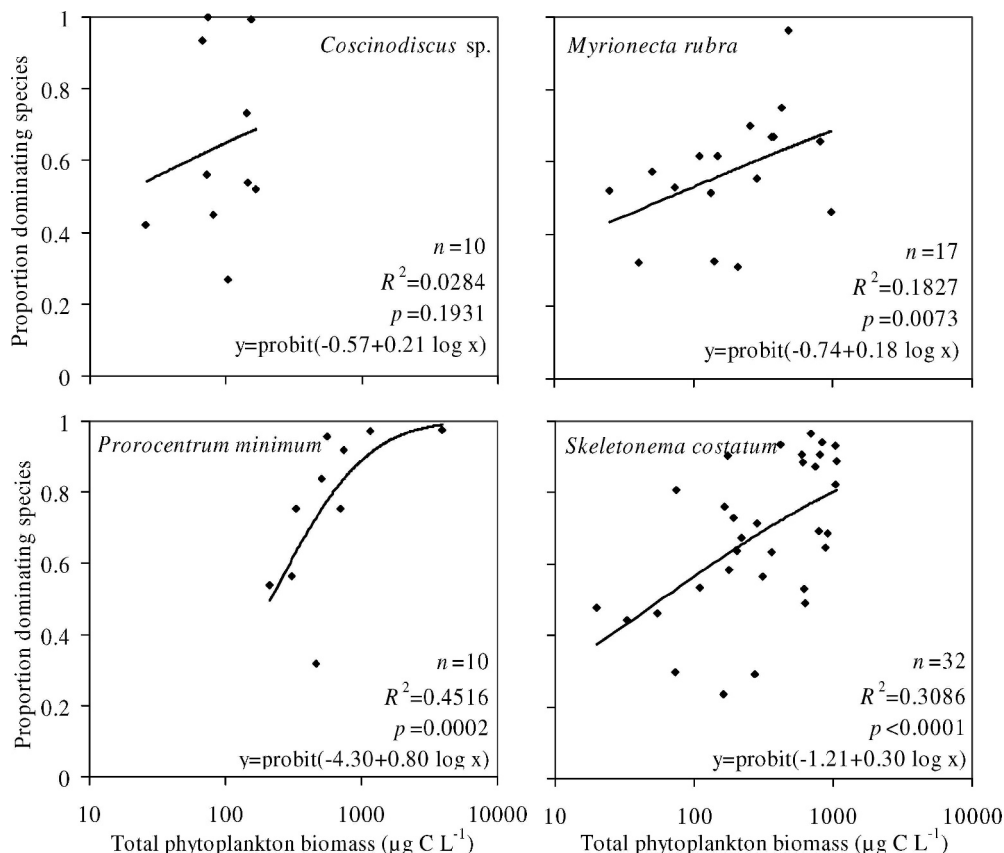

Fig. 7. The biomass proportion of the four most dominating species related to total biomass (bloom observations only). Total phytoplankton biomass is on logarithmic scale.

Table 6.   Species-specific increases in biomass proportion at summer bloom initiation. n is the number of bloom initiations (pairwise observations from nonbloom to bloom situation with less than 14 d in between, total of 78) where the species was observed in either of the samples. $P_{increase}$ is the frequency of increases in biomass proportion ($n_{increase}/n$), and p is the probability that $P_{increase} = 0.5$. Statistics are shown for species with $n \geq 20$ only. Species are ranked by the mean change in biomass proportion. Significant sign tests are accentuated in bold.

	Frequency of change			Change in biomass proportion		
Species	n	$P_{increase}$	p	Median	Average	Maximum
Skeletonema costatum	72	55.6%	0.4096	1.09%	11.29%	86.92%
Prorocentrum minimum	23	73.9%	**0.0347**	0.04%	8.34%	78.60%
Chaetoceros socialis/radians	24	75.0%	**0.0227**	0.13%	5.60%	63.50%
Heterocapsa triquetra	29	69.0%	0.0614	0.03%	5.51%	89.93%
Cerataulina pelagica	29	79.3%	**0.0023**	0.42%	3.35%	36.88%
Ditylum brightwellii	20	65.0%	0.2632	0.18%	2.77%	39.35%
Rhizosolenia setigera	20	55.0%	0.8238	0.03%	1.35%	20.73%
Rhizosolenia delicatula	23	65.2%	0.2100	0.03%	0.58%	10.88%
Prorocentrum micans	21	76.2%	**0.0266**	0.32%	0.52%	43.10%
Dinophysis acuminata	27	59.3%	0.4421	0.04%	0.10%	1.44%
Nitzschia longissima	45	55.6%	0.5515	0.00%	0.00%	5.50%

blooms because the problems associated with blooms do not relate to biomass only. However, quantitative analyses on other bloom descriptors, such as harmfulness and toxicity, may provide similar definitions that contribute to characterizing the bloom problem in addition to the biomass definition. It is most unlikely that everything a phytoplankton bloom entails can be encapsulated in a single number only, but this should not prevent science from developing quantitative measures that deliver answers to one side of this multifaceted problem. Therefore, in this paper we focus on the biomass levels only and present an approach to categorize phytoplankton biomass observations into blooms and nonbloom events, assuming that biomass peaks defined as blooms deviate from the normal seasonal cycle of phytoplankton biomass levels. Moreover, we claim that the quantitative bloom definition on the basis of biomass allows for investigating the underlying mechanisms driving phytoplankton dynamics, as well as the evaluation of the consequent effects of increased phytoplankton production to the other parts of the ecosystem. Further, the biomass approach we present here allows adaptation of the bloom concept to a region or type-specific conditions, enabling development of regional criteria for bloom frequencies and linking with information on nutrient loading and other pressure information for development of management plans.

Chl *a* concentrations have often been described by the lognormal distribution because observations were right-skewed (Tett and Wallis 1978). We suggest that the cause of this skewness derives from two different underlying distributions. Therefore we have developed a general algorithm to categorize time series of Chl *a* concentration into observations of blooms and nonblooms, assuming nonblooms to be described by a normal distribution with a seasonal mean and observations deviating from this distribution were blooms. The definition is more flexible than commonly used threshold values for phytoplankton blooms that allow for neither seasonal nor spatial variations, and can be applied to Chl *a* data from different

regions provided that sufficient data are available to characterize the nonbloom distribution.

Mechanisms of phytoplankton summer blooms—Increases in phytoplankton biomass leading to blooms must arise from a positive growth, low contribution of loss processes (e.g., grazing, dissolution, sedimentation), or transport terms in the mass balance. We suggest the following five mechanisms for establishment of summer blooms in temperate, shallow estuaries: (1) external inputs of nutrients from land, atmosphere, or sediments converted into biomass through active growth; (2) enhanced growth through improved light conditions; (3) decoupling of benthic suspension feeders and pelagic grazers resulting in phytoplankton biomass accumulation; (4) advective transport from areas with a higher biomass; and (5) resuspension of benthic algae into the water column.

Light attenuation measurements have been carried out in DNAMAP since 1998 and daily irradiance levels averaged over the upper mixed layer were almost permanently above 100 μmol m^{-2} s^{-1} from May to August at all stations (data not shown), i.e., well above the range of light limitation for common estuarine species (e.g., Langdon 1987; Thompson et al. 1989). Thus, summer blooms were unlikely caused by enhanced light conditions.

Phytoplankton growth was therefore considered nutrient limited or controlled by grazing during the summer period. The significant increases in total nutrients during blooms at six of the nine stations indicate an external input of nutrients to the water column. The low bottom oxygen concentration in the previous sample at station 3727 (Table 4) suggests that nutrient releases from the sediments under hypoxic conditions could be a major cause for summer blooms. The parts of Limfjorden associated with station 3723, 3708, and particularly 3727 are frequently exposed to hypoxia in July and August. The correlation in time between bloom observations at these three stations (Table 3) signifies that the bloom mechanisms are similar. Moreover, our data suggest that the bloom intensity
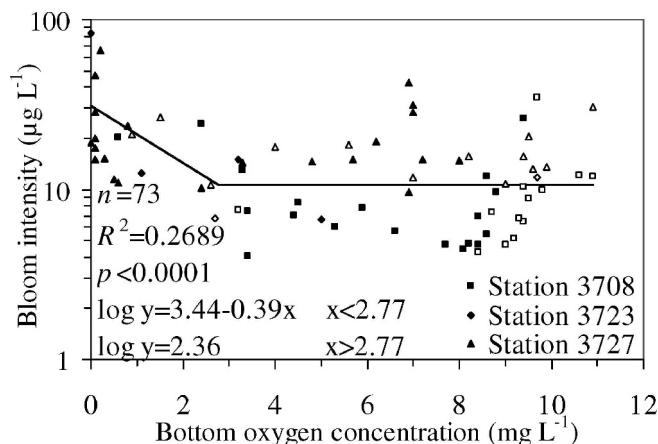
Fig. 8. Nonlinear model for bloom intensity versus bottom oxygen concentration at three central stations in Limfjorden. Open and closed symbols show observations from May through June and July through August, respectively. The threshold model was estimated by nonlinear regression using a likelihood ratio test for significance.

increased significantly as oxygen concentration got below a certain threshold (Fig. 8). However, other mechanisms must account for the majority of blooms in May and June when hypoxic events are rare. Nutrients can also be released to the water column through resuspension of the sediments, as will the benthic algae on the sediment surface. Higher wind conditions before the bloom observations and increases in TP suggest this combined mechanism to be important in the relatively shallow and wind-exposed western part of Limfjorden (station 3702).

If the phytoplankton community is nutrient limited the concentrations of inorganic nutrients would be low for both bloom and nonbloom observations. At three stations (3711, 4273, and 60) there was a substantial decrease in DIN and DIP for bloom observations (Table 4) while total nutrients remained at the same level, showing that the bloom was caused by transforming inorganic nutrients into biomass without any significant external input of nutrients. Furthermore, mean DIN and DIP concentrations for nonbloom observations were well above levels associated with nutrient limitation (Fisher et al. 1992), whereas phytoplankton growth was potentially limited by nutrients during blooms. This indicates that phytoplankton was grazer-controlled during nonblooms while decoupling of benthos during periods of stratification allowed for bloom development. Although blooms were not more frequent when the water column was stratified, depth-specific gradients in phytoplankton biomass can develop when turbulent mixing is low (Huisman et al. 1999). Low winds prior to blooms at station 60 and 3711 confirm that the water column was probably more stable, allowing phytoplankton to escape the filter feeders, as has been suggested by Møhlenberg (1995) for Roskilde Fjord.

Dolmer (2000) documented large differences in phytoplankton abundance (factor 3–10) within 2 m above the mussel-filled bottoms in Limfjorden. Danish estuaries have a high abundance of filter-feeding bivalves, particularly the blue mussel *Mytilus edulis*, and mussel harvesting is
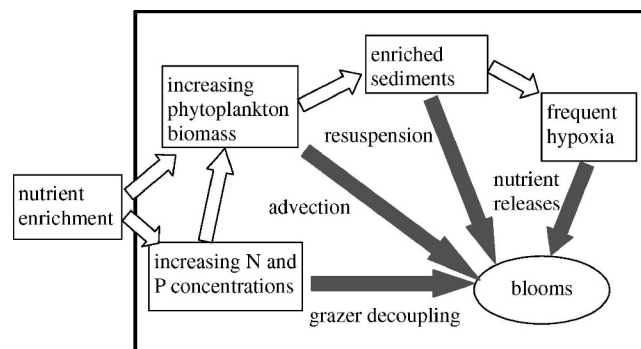

Fig. 9. System-specific conceptual model of summer bloom mechanisms linked to nutrient enrichment. Increased nutrient concentrations in the water column and sediments, increased phytoplankton biomass, and increased frequency of hypoxia create a potential for blooms that are triggered by meteorological conditions. Decoupling of benthic grazers by stratification allows phytoplankton to use the inorganic nutrient pool to develop a bloom. Blooms can be advected from areas with high phytoplankton concentration. Nutrients and phytoplankton can be resuspended from the sediments to develop a bloom. Hypoxia causes nutrient releases from the sediments that can fuel phytoplankton blooms.

intensive in Limfjorden, Vejle Fjord, and Kolding Fjord (Conley et al. 2000). Although benthic grazing may not appear important in those deeper parts of Limfjorden frequently exposed to hypoxia, the extensive shallow shoals bordering these areas are most likely regulated by mussels.

The proximity to freshwater sources within estuaries creates natural gradients for salinity, nutrients, and Chl *a*. Decreasing salinity and increasing total nutrients at stations 3711, 4273, 5790, and 6900017 indicate that blooms could be caused by advective transport from the inner part of the estuary. In fact, all stations showed decreases in salinity before blooms, suggesting that advective transport is a bloom mechanism found in most estuaries, particularly those with a large freshwater input (Pinckney et al. 1997).

Our study shows that there are large spatial differences in the underlying bloom mechanisms, perhaps even on a small scale within estuaries, and that site-specific features do not prescribe a single main mechanism for bloom initiation. Tidal forcing, not considered in the present study, is another important mechanism enhancing bloom development in combination with other factors (May et al. 2003). Consequently, the diversity of the driving factors, modulated by a wide variety of system-specific attributes (Cloern 2001), illustrates the complexity of understanding summer bloom mechanisms in shallow estuaries, as opposed to the more simple mechanism observed in open, permanently stratified waters (Carstensen et al. 2004).

Summer blooms and nutrient enrichment—Despite this complexity of bloom mechanisms our conceptual understanding of estuarine ecosystems still prescribes a link between nutrient enrichment and bloom frequency and intensity (Fig. 9), although the link depends on system-
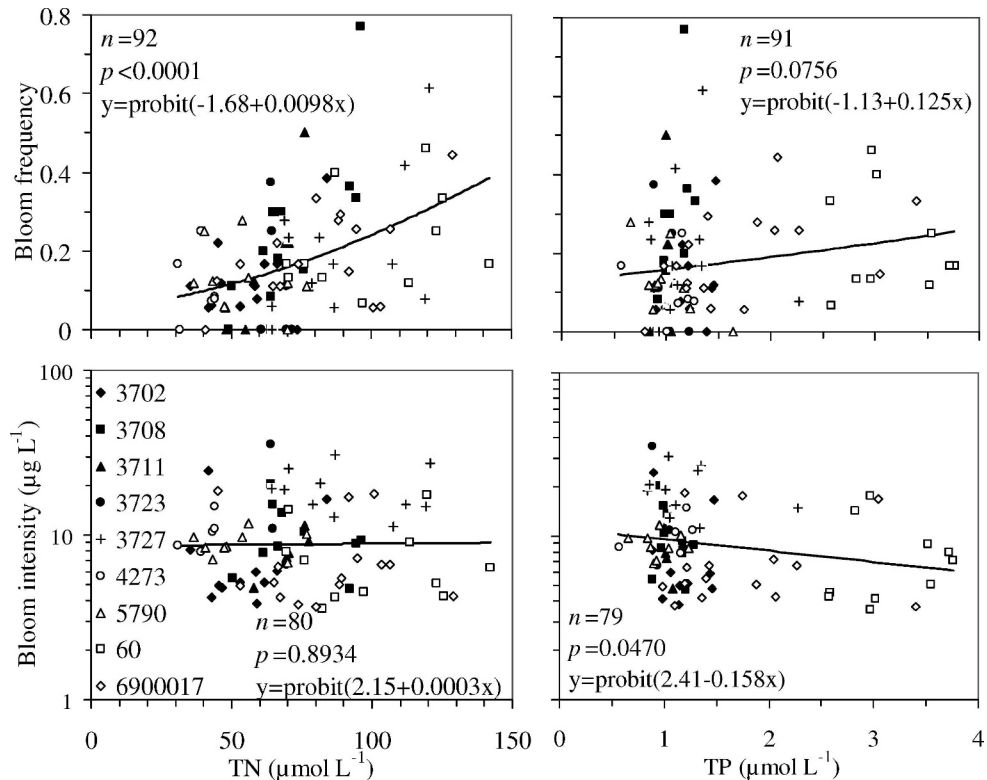
Fig. 10.   Summer bloom frequency and intensity related to mean nutrient levels (January–April) at the nine stations. Regressions were modeled within the framework of generalized linear models. Outlier TN (1 obs.) and TP (2 obs.) means are not shown in the plots and were not included in the regressions. Bloom intensity is shown on a logarithmic scale.

specific features such as retention time, water depths, stratification pattern, wind fetch, and estuarine circulation. The decreasing trends in bloom frequency and intensity occurred in the same period as both nitrogen and phosphorus inputs to Danish marine waters decreased (Carstensen et al. 2006). The summer bloom frequency increased with TN levels in the winter–spring period, whereas bloom intensity was not related to nutrient levels (Fig. 10). The magnitude of the summer blooms was station-specific only ($\chi^2 = 34.99$, $p < 0.0001$, $n = 81$, df $= 8$), with the highest levels at stations prone to events of hypoxia. Thus, although there is a conceptual link between bloom intensity and nutrient enrichment (Fig. 9), this relation is masked by larger site-specific variations.

The identified relation with TN documents that bloom frequency can be used as an ecological indicator in relation to eutrophication, but the complexity of bloom mechanisms, evident by the large variation around the regression line, questions if bloom frequency is also a precise indicator for assessing ecological status. Including site-specific features combined with data on driving forces, typically wind, may reduce the random variation, at the cost of indicator generality. Thus, the frequency of summer blooms in Danish estuaries is most likely higher today than under pristine conditions, but it will require large amounts of data (as in the present study) and large changes in nutrient conditions to document significant changes.

Composition of summer blooms—The main bloom-forming species found in the Danish estuaries are common to temperate coastal areas and estuaries (e.g., Cloern and Dufford 2005) and the dinoflagellates contributing highest biomasses to the blooms were all representatives of types I and II sensu Smayda and Reynolds (2003) typically found in near-shore blooms.

The stations included in the present study represent areas with average summer salinities ranging from ca. 12–14 (station 60) to 30–32 (station 3702). Phytoplankton community structure is dependent on salinity (Gasiunaite et al. 2005) and therefore the occurrence of specific species in summer blooms will at first be related to their physical requirements for growth. While e.g., *Skeletonema costatum* that is able to grow across a wide range of salinities (5–32, Cloern and Dufford 2005) was found to be the dominant species in blooms from all stations, other species like *Rhizosolenia fragillissima* and *Cerataulina pelagica* require higher salinity and do not form blooms in the areas of low salinity (only dominating at salinities above 20).

The assembly of species contributing most to the biomass of blooms (Table 5) comprised generally fast-growing diatoms and flagellates and a selection of some of the fastest growing dinoflagellates (Smayda 1997*b*). This could indicate that blooms represent situations where growth conditions become beneficial and fast-growing opportunistic species immediately exploit an open niche.

It is noteworthy, however, that in the cases where a comparison of dominance before and during blooms was possible, the biomass proportion of the dominant species on average increased very little (<12%, Table 6) during the buildup of blooms. Thus, rather than a complete takeover of the phytoplankton community by a single species during the initiation of blooms, the general environmental conditions of the water body and biological interactions select for species that constitute a substantial component of the phytoplankton and may develop further into unusual high biomasses (blooms) given a beneficial change in growth conditions, e.g., external nutrient inputs or release of grazing pressure. This observation is also supported by evidence from mesocosm experiments, where nutrient enrichments were exploited by phytoplankton species already having a relatively high share of the initial community, and even more intensive blooms were formed in enclosures where grazing pressure was suppressed (Olli et al. 1996).

Danish coastal waters and estuaries are characterized by low concentrations of DIN during the summer period (Conley et al. 2000). Thus the chemical environment would be expected to select for species with high affinity for nutrients as is also indicated by the dominance by diatoms in the majority of blooms (50–86%) at all stations but station 60 (39%). In general diatoms have lower half-saturation constants for nutrient uptake than dinoflagellates and other phytoflagellates (Smayda 1997*b*) and diatoms respond rapidly to nutrient pulses (Cloern and Dufford 2005). Unlike at most of the stations, blooms at station 60 (61% dominated by nondiatoms with assumed relatively higher half-saturation constants for nutrient uptake) were associated with very small and insignificant increases in total nutrients and presumably related to released grazing pressure from benthic mussel beds.

In addition, top-down control of phytoplankton by benthic grazers and the composition of and selective grazing by the pelagic meso- and microzooplankton community will influence the phytoplankton species composition. It is unknown to what extent the trophic interactions have affected the observed species composition patterns of summer blooms.

In summary, we propose a statistical approach for identification of bloom observations in long-term monitoring data. The approach is relatively simple and can be applied to other ecosystems, provided that sufficient data are available for characterizing the normal phytoplankton cycle. The definition can be used for investigating the underlying mechanisms of blooms by analyzing the hydrophysical and chemical regimes, as well as changes in the phytoplankton composition.

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